

Abstract. – Age, growth, and reproduction were studied in goosefish *Lophius americanus* collected from National Marine Fisheries Service groundfish surveys and commercial fishing cruises between Georges Bank and Cape Hatteras in the western North Atlantic. Age and growth of *L. americanus* were determined from vertebral annuli, which became visible at the edge of the vertebral centra in May. Maximum ages of males and females were 9 and 11 years, respectively. Males appeared to experience higher mortality than females in the older age-classes. Von Bertalanffy growth curves calculated for males and females had excellent agreement with back-calculated lengths. The growth rate of *L. americanus* was intermediate to its eastern Atlantic congeners, *L. piscatorius* and *L. budegassa*. Male *L. americanus* matured at 3+ years (~370 mm TL) and females at 4+ years (~485 mm TL). Spawning took place primarily in May and June. Fecundity in 17 individuals of 610–1048 mm TL ranged from 300,000 to 2,800,000 ova, and was linear with total length in that size range. Histological examination of the ovaries showed they are remarkably similar to ovaries of other lophiiform species. Females produced egg veils, which may function in dispersion, buoyancy, facilitating fertilization, and protection of the eggs and larvae.

Age, growth, and reproduction of the goosefish *Lophius americanus* (Pisces:Lophiiformes)*

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The goosefish *Lophius americanus* (Valenciennes in Cuvier and Valenciennes 1837) is a benthic fish which occurs in the Northwest Atlantic Ocean from the northern Gulf of Saint Lawrence, southward to Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Scott and Scott 1988) and less commonly to Florida (Caruso 1983). It has a eurybathic depth distribution, having been collected from the tideline (Bigelow and Schroeder 1953) to approximately 840 m (Markle and Musick 1974), although few large individuals occur deeper than 400 m (Wenner 1978). Goosefish have been taken in temperatures of 0–24°C (Grosslein and Azarovitz 1982), but seem to be most abundant in temperatures of about 9°C in the Mid-Atlantic Bight (Edwards 1965), 3–9°C in Canadian waters (Jean 1965), and 7–11°C on the continental slope off Virginia (Wenner 1978). The goosefish is sympatric with the black-finned goosefish *L. gastrophysus* in deep water (>100–150 m) from Cape Hatteras to the Florida coast, although strays of *L. gastrophysus* occur as far north as Washington Canyon, off Virginia (pers. observ., MPA).

Lophius americanus was confused with *L. piscatorius*, a European species, for many years. Thus all references to *L. piscatorius* in the western North Atlantic north of Cape Hatteras actually refer to *L. americanus* (Caruso 1977). There are several accounts of the species' life history (Gill 1905, Connolly 1920, Dahlgren 1928, Hildebrand and Schroeder 1928, Proctor et al. 1928, McKenzie 1936, Bigelow and Schroeder 1953, Grosslein and Azarovitz 1982, Scott and Scott 1988), but all are general in nature. Much of the information contained in these reports is anecdotal.

Goosefish are a bycatch of ground-fishing and scalloping operations and are marketed under the name monkfish. They have traditionally been considered "trash" fish in the United States and discarded at sea or used in the production of fish meal, with a small amount being exported to Europe where *Lophius* has been highly esteemed as a food fish for centuries. Goosefish have become more popular with the American consumer due to dwindling catches and rising prices in recent years of the more traditional fishery products. Commercial landings have been increasing yearly since 1970 (Northeast Fisheries Science Center 1991). This

study describes age, growth, and reproduction of this increasingly exploited fish.

Methods

Goosefish were collected during the spring and autumn groundfish surveys (1982–85) conducted by the National Marine Fisheries Service (NMFS) in the Mid-Atlantic Bight and southern New England (for survey methodology see Grosslein and Azarovitz 1982). Additional samples were obtained during the NMFS 1983 summer scallop survey off southern New England and during cruises aboard commercial groundfish trawlers and scallopers operating out of Hampton, Virginia. Sampling effort was concentrated in the area from southern New England to Virginia.

Goosefish greater than ~180 mm were examined at sea. Smaller individuals were fixed in 10% formalin and saved for examination in the laboratory. Examination included measuring total and standard length and weight, excising a section of the vertebral column, removing both sagittal otoliths, recording stomach contents, macroscopic staging and weighing of the gonads, and preserving pieces of gonads for histological inspection and fecundity estimates.

Reproduction

Gonads were staged visually in the field and assigned to one of the following classes: immature, resting, developing, ripe, and spent. Both gonads were then removed from the body cavity and weighed to the nearest 0.1 g. A small representative piece was excised from the midsection of selected gonads and preserved in Davidson's fixative for histological study.

Late-developing and ripe ovaries were selected for fecundity analyses. The extremely large size of goosefish ovaries precluded saving the entire organ. A subsample of about 100 g was weighed to the nearest 0.1 g and placed in modified Gilson's solution (Simpson 1951). After several months of storage, most of the ovarian connective tissue had dissolved. Ova were removed from the Gilson's solution, separated from any remaining ovarian tissue, rinsed in water, blotted on absorbent paper, and weighed. Three subsamples, each containing about 1000 ova, were removed and weighed to the nearest 0.001 g. Ova in each sample were counted using a dissecting microscope. Fecundity was calculated as:

$$\text{Fecundity} = (W)(P)(N)$$

where W = total weight of both ovaries,
 $P = \frac{\text{weight of sample after Gilson's}}{\text{weight of sample before Gilson's}},$

N = mean number of ova/g from 3 subsamples.

Gonad portions preserved in Davidson's fixative for histological preparations were dehydrated in a graded series of ethanol baths and Technicon reagents (S-29 dehydrant VC-670 solvent). They were then embedded in paraffin, sectioned at 7 μm and stained using Harris' hematoxylin and counterstained with eosin Y. Gonad sections were viewed at 40 \times , 100 \times , and 400 \times to determine stages of oogenesis and spermatogenesis to verify accuracy of macroscopic field staging and to examine the histology of the goosefish ovary.

A gonasomatic index (GSI) was calculated for each sex as:

$$\text{GSI} = \frac{\text{gonad weight}}{\text{total weight of fish}} \times 100.$$

Age and growth

Weights were taken to the nearest gram in fish <1200 g and to the nearest 25 g increment in fish >1200 g. Total length (TL) in millimeters was measured from the tip of the protruding lower jaw to the tip of the caudal fin rays. Because of the large size and loose suspension of the goosefish jaw apparatus, it was necessary to hold the head in a standard position while length was measured to reduce variation due to changes in head and jaw configuration. This position was achieved by applying light pressure to the top of the head, thereby causing a maximal amount of dorsal-ventral compression.

Vertebrae were chosen as the best method to age *L. americanus*, based on a preliminary examination which revealed that each vertebral centrum contained concentric rings which appeared to be annuli. Sagittal otoliths were also examined; however, otoliths from larger fish were opaque and had extremely irregular outer margins, which made it difficult or impossible to discern annuli.

A section of the vertebral column containing vertebrae numbers 3–11 was excised from each goosefish. These were stored in 50% isopropanol for 1–12 months. Vertebrae numbers 7–10 were similar in size and shape and also had the largest diameters. Vertebra number 8 was used in aging, but number 9 was used if number 8 was damaged in preparation.

Vertebra number 8 was disarticulated from the rest of the excised vertebral section. The neural and haemal arches and all excess fat, muscle, connective tissue and cartilage were removed by scalpel. The vertebra was then sliced along the midsagittal line producing two hourglass-shaped halves, similar to the method used by Lyczkowski (1971) and Lawler (1976) for preparing vertebrae from northern puffer *Sphaeroides maculatus*.

and sandbar sharks *Carcharinus plumbeus*. These halves were then heated in an oven at 200°C for about 3 hours. Larger vertebra required one-half to 1 hour further heating. This heating made the alternating opaque and translucent bands of the vertebral centra more distinct.

Annuli were counted on the posterior face of the centrum. This was generally more concave than the anterior face, thus allowing greater separation of the rings. Each vertebra was read twice at an interval of at least one month to insure independence of readings. If they disagreed, a third reading was done. Agreement between any two readings was considered as the true count. If all three readings differed, the vertebra was considered unreadable and not used in the analysis. A random sample of fifty vertebrae was selected for verification by an independent reader.

Measurements of the vertebral rings and radius were made from the apex of the posterior and anterior faces of the centrum along an oblique line that followed the midline of the posterior centrum. All measurements and counts were made with a binocular dissecting microscope equipped with an ocular micrometer at 10× magnification using reflected light.

Regression analyses of vertebral radius on total length and weight on total length were calculated by the method of least squares. Length-at-age was back-calculated by the Lee method (Lagler 1956):

$$L' = C + S' (L - C)/S$$

where L' = total length of the fish at time of annulus formation,

L = total length of fish at time of capture,

S' = measurement to the annulus,

S = vertebral radius at time of capture,

C = correction factor; y-axis intercept of the regression of total length on vertebral radius.

Computation of the von Bertalanffy growth equations followed Ricker (1975).

Results

Reproduction

External sexual dimorphism was not apparent in *L. americanus*. Caruso (1975) noted sexual differences in nostril morphology, but this was not a useable field character. Sex was easily determined in mature individuals by examination of the gonads, which are markedly different in appearance. Gonads from small juveniles (<160–180 mm TL) were indistinguishable macroscopically. Both testes and ovaries from these juveniles were small, translucent, and string-like.

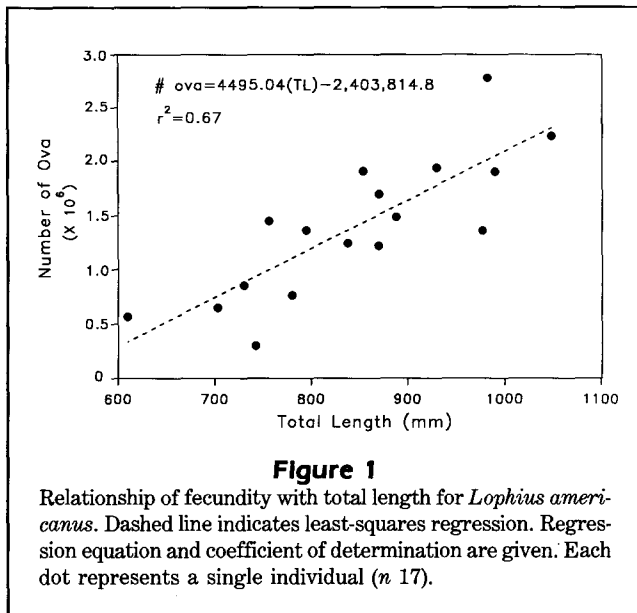
In females larger than ~180 mm TL the ovaries were long, wide, and ribbon-like. They were greatly coiled in the abdomen and supported by an extensive mesovarium. The two ovaries were fused at their posterior ends, forming a single, confluent organ. Dimensions of the ovary varied greatly depending on the stage of sexual development.

The testes were solid, sausage-like organs. A groove was present along the medial aspect of each testis. This groove contained blood vessels and served as the site of attachment for mesentery connective tissue.

A physical description of the gonads in the five developmental stages (immature, resting, developing, ripe, and spent) is presented in Table 1.

Table 1
Description of gonads at five maturity stages assigned to *Lophius americanus*, based on macroscopic examination.

Stage	Description
Ovaries	
Immature	Grayish-pink, relatively small, ribbon-like, appear almost empty, no vascularization.
Resting	Orangish-pink, contain material but no ova visible, larger than immature, little vascularization.
Developing	Pink, ova discernible by eye, abdominal cavity slightly bulging, highly vascular.
Ripe	Straw-colored to almost clear as ovary approaches spawning, distinct ova present, abdominal cavity greatly bulging, highly vascular.
Spent	Gray, extremely flaccid, appear almost empty, atretic ova appear as black or white dots, moderately vascular.
Testes	
Immature	White to tan, similar in shape as mature testes but very small, medial groove less distinct.
Resting	White to tan, much larger than immature, medial groove distinct, small amount of milt sometimes present when dissected.
Developing	Blotchy cream to tan, moderate to large amount of milt produced when dissected, very firm in texture.
Ripe	Blotchy cream to tan with areas of pink, extremely firm in texture, milt produced from genital pore when pressure is applied on abdomen, copious amounts present when dissected.
Spent	Grayish-tan, edges appear translucent, extremely flaccid, small amount of milt sometimes present when dissected.



Fecundity in 17 individuals of 610–1048 mm TL ranged from 301,150 to 2,780,632 ova. Fecundity increased linearly with TL in that size range (Fig. 1), the regression equation being

number of ova =

$$4495.04(TL) - 2,403,814.8 \quad (r^2 = 0.67).$$

Log transformations of one or both variables failed to provide a better fit.

Goosefish reached sexual maturity (by macroscopic staging) at 290–450 mm in males and 390–590 mm in females (Fig. 2). Linear regressions of proportion mature (arcsine-square root transformed) on TL for these size intervals were:

Proportion of males mature =

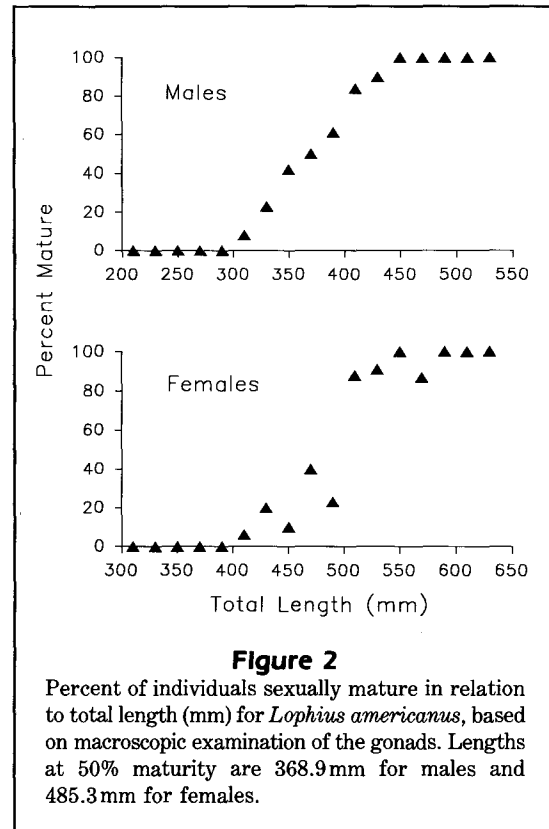
$$0.0089(TL) - 2.498 \quad (r^2 = 0.96)$$

Proportion of females mature =

$$0.0079(TL) - 3.056 \quad (r^2 = 0.86).$$

Values for length at 50% maturity were 368.9 mm in males and 485.3 mm in females.

Ovaries and testes followed similar patterns of development, with the exception that testes changed from a resting to developing state earlier in the year (Jan.–Feb.) (Fig. 3). No resting gonads were found for either sex in May or June. The percentage of spent gonads was highest in July–August, indicating that spawning had taken place in the previous time interval (May–June). Although the percentage of ripe gonads was

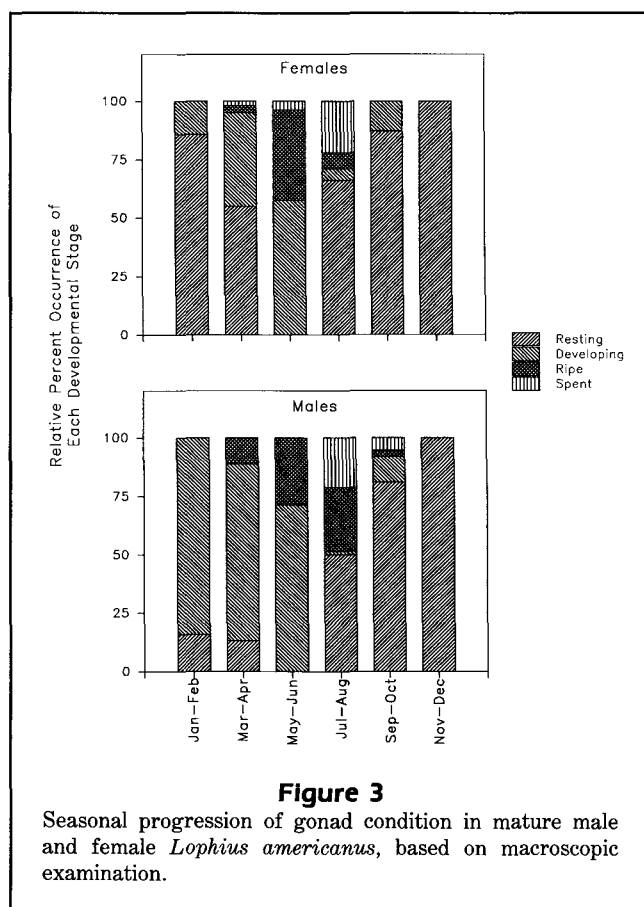


highest in May–June, gonads in a near-spawning state were also found in March–April and July–August.

Gonasomatic values were calculated for 117 mature males and 98 mature females. The GSI peaked in May–June for females and March–April and May–June for males (Fig. 4). High index values in these months corresponded with the greatest incidence of ripe individuals (Fig. 3). Again, similar to observations based on gonad condition, males appeared to develop earlier in the season and remain ripe longer. No mature females were collected during the Jan.–Feb. interval.

GSI values for females were much greater than for males (Table 2). Females showed a large increase in GSI as the ovaries developed. The greatest value recorded was 50.9, from a ripe female. This value indicates that greater than half of the body weight was composed of ovarian mass. However, only a relatively small percentage of the ovarian weight from late-developing and ripe females was composed of ova. The actual percentage of the ovarian weight which was ova ranged from 12.9% to 33.5% for the seventeen females used for fecundity analysis. The remainder of the weight was ovarian tissue, and more importantly, the muco-gelatinous matrix surrounding the ova.

Slides were prepared from sections of 33 ovaries and 20 testes. Representatives from all the developmental



classes (immature, resting, developing, ripe and spent) were included.

Oogenesis proceeds through six distinguishable morphological stages similar to other fishes, such as black sea bass *Centropomus striata* (Mercer 1978):

Oogonia (4.5–11 μ m) Densely packed, granular, deeply basophilic cells.

Stage 1 Small (15–50 μ m) oocytes with a large nucleus, single nucleolus, and small amount of basophilic cytoplasm.

Stage 2 (30–200 μ m) Previtellogenic oocytes with strongly basophilic cytoplasm and multiple nucleoli around the nucleus margin.

Stage 3 (110–390 μ m) Vitellogenesis begins with the deposition of yolk vesicles in the less darkly-staining cytoplasm. A thin zona radiata can be seen in late stage-3.

Stage 4 (270–970 μ m) Cytoplasm filled with yolk vesicles and globules, lightly staining. Zona radiata well developed and strongly acidophilic.

Stage 5 (>600 μ m) Mature or nearly mature oocytes, uniform in appearance due to the coalescence of yolk globules. Often fractured or irregular in outline due to fixation and sectioning.

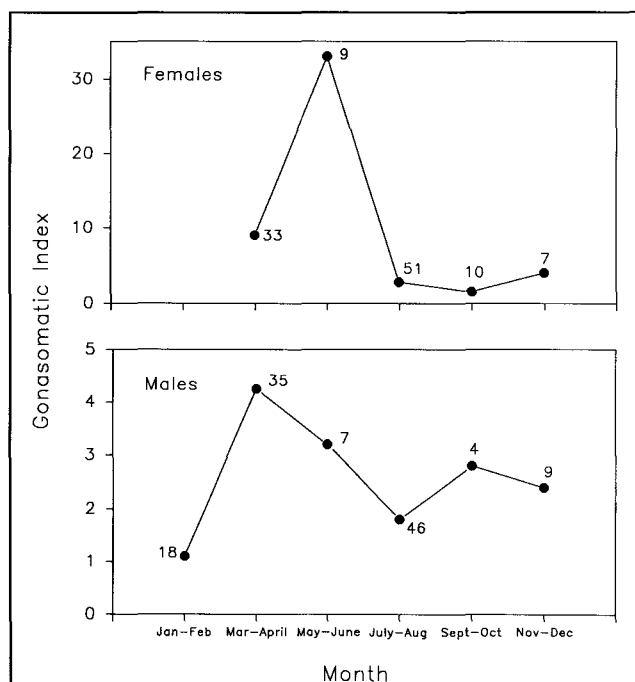


Table 2

Gonosomatic index values at five gonad maturity stages for male and female *Lophius americanus*, based on macroscopic staging.

	Range	Mean(SE)	n
Females			
Immature	Trace–1.26	—	56
Resting	0.77–7.58	2.35(0.19)	53
Developing	3.82–22.12	12.26(1.18)	21
Ripe	18.23–50.90	33.96(2.73)	13
Spent	0.94–3.77	2.56(0.43)	12
Males			
Immature	Trace–0.83	—	37
Resting	0.31–3.42	1.46(0.17)	36
Developing	0.46–6.18	2.44(0.27)	43
Ripe	0.84–5.72	3.20(0.22)	23
Spent	0.18–4.19	1.16(0.20)	21

Based on the occurrence of these oocyte stages, the ovaries were placed in the following developmental classes:

Immature Stage 1 and 2 oocytes present, atretic bodies absent. The ovarian lamellae are pressed tightly together and lumen is small.

Resting Stage 1, 2, and 3 oocytes are present with stage 2 dominating.

Developing Oocyte stages 1, 2, 3, and small 4 are present with 3 dominating.

Ripe Oocyte stages 1, 2, 3, 4, and sometimes 5 are present with 4 dominating.

Spent Oocyte stages 1, 2, and 3 are present with 2 dominating. Atretic stage 4 and 5 oocytes and ruptured follicles are present.

Macroscopic and microscopic maturity classifications showed excellent agreement. Only two (6%) needed to be reclassified following histological examination. These included one reclassified from ripe to developing, and one from resting to immature.

Figures 5 and 6 show the histology of the ovary. The lumen is not centrally located but is at one side (Fig. 5). The ovigerous tissue extends into the lumen in the form of lamellae from one wall only. In late-developing and ripe ovaries, the mucogelatinous material that forms the egg veil can be seen surrounding the ovigerous lamellae and filling the lumen (Fig. 6). This material is produced by the epithelial cells (Fulton 1898), which can be seen lining the lumen and lamellae (Fig. 6).

Spermatogenesis proceeds through six distinct stages analogous to those described for *Tilapia* spp. (Hyder 1969) and *Caulolatilus microps* (Ross 1978). These stages are primary and secondary spermatogonia, primary and secondary spermatocytes, spermatids, and spermatozoa. Spermatogenesis in goosefish is not notably different from other teleosts, so the process is not described here.

The 20 testes examined histologically were placed in the following maturity classifications based on a modification of the system of Hyder (1969):

Immature Primary and/or secondary spermatogonia are

present; primary and/or secondary spermatocytes may also be present.

Resting Primary and/or secondary spermatogonia and spermatocytes are present. Spermatids also

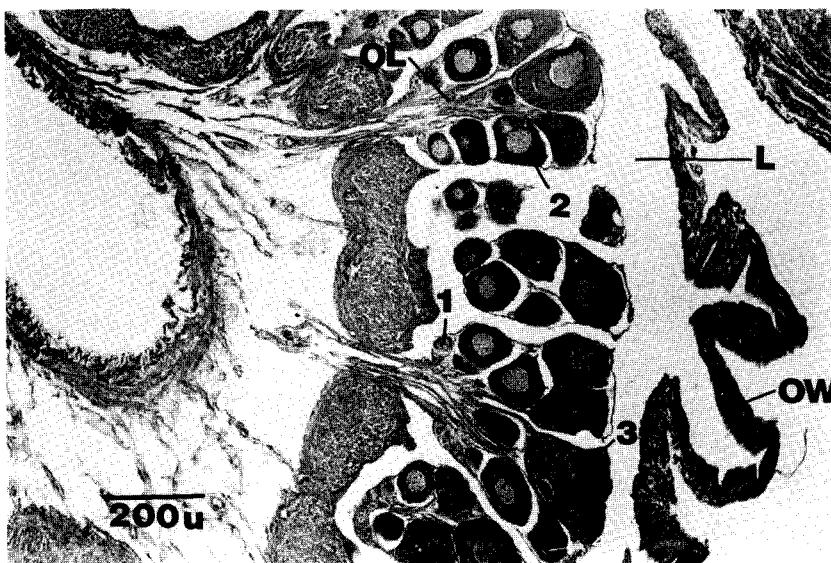


Figure 5

Photomicrograph of *Lophius americanus* ovary, classified as resting (40 \times): OL = ovigerous lamella; L = lumen of ovary; OW = nonovigerous ovarian wall; 1-3 = stages of oocyte development.

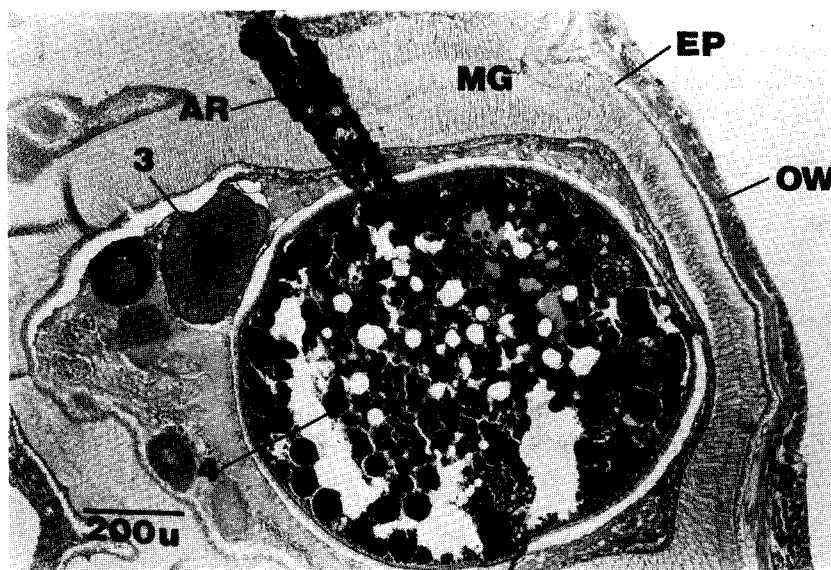


Figure 6

Photomicrograph of *Lophius americanus* ovary, classified as late developing (40 \times): MG = mucogelatinous matrix; EP = epithelial lining of lumen and lamellae; OW = nonovigerous ovarian wall; AR = artifact; 3-4 = stages of oocyte development.

present. Small amount of spermatozoa may be present in lumen.

Developing Few primary and/or secondary spermatogonia visible; primary and/or secondary spermatocytes and spermatids present; spermatozoa present in lumen.

Ripe Few or no primary and/or secondary spermatogonia and spermatocytes visible; lumen densely packed with spermatozoa.

Spent No primary and/or secondary spermatogonia or spermatocytes visible; no spermatids present; few spermatozoa remaining in lumen.

In all cases, maturity classifications based on histological examination agreed with visual classifications applied in the field.

Age and growth

Growth marks on the vertebrae of *L. americanus* formed distinct steps on the centrum surface. Under magnification in reflected light, the surface texture of the step appeared coarser than the rest of the centrum. A narrow, dark, translucent band was on the outer side of each step. The step and the narrow band formed a continuous ring around the centrum and was considered to be the annulus. Broader, lighter opaque bands with relatively uniform surface texture were between the annuli. A broad, opaque band combined with a narrow, translucent band and step was interpreted as one year's growth. While these features were visible on fresh vertebrae, they became much more distinct when the vertebrae were heated. The step became deeper and the narrow, translucent band became opaque and dark relative to the rest of the centrum (Fig. 7).

Annuli were counted on vertebrae from 635 goosefish. In 200 (31.5%) cases, the first and second reading did not agree and a third reading was done. In most cases, the second reading differed by only one. In 25 (3.9%) cases, the third reading was different from both the first and second; these vertebrae were considered unreadable and discarded from the analysis.

Differences between readings were due to the presence of false annuli or because the true annuli were not distinct. False annuli appeared as dark bands but were not associated with a step. Another extraneous mark that sometimes occurred was a depression that formed a continuous ring on the centrum but was not a defin-

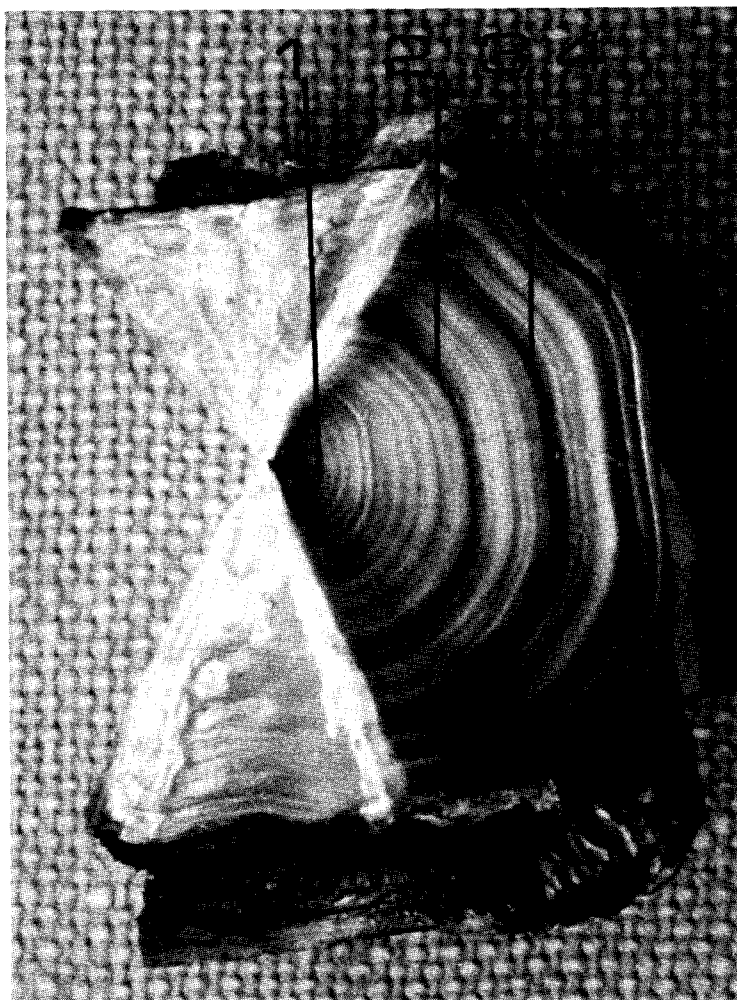


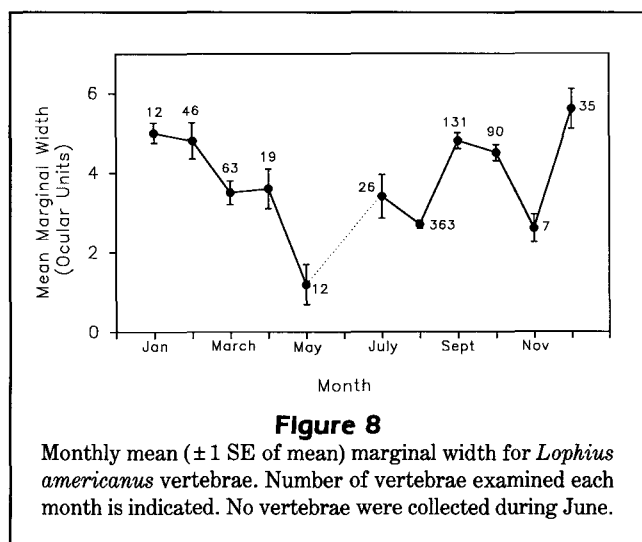
Figure 7

Vertebra from a 4-year-old *Lophius americanus*, after heating. Annuli are indicated.

itive step. This feature has also been found on black bullhead (Lewis 1949) and northern puffer (Lyczkowski 1971) vertebrae.

Annuli counts determined by the independent reader agreed with the original counts in 40 (80%) cases. In no case did the counts differ by more than one.

Van Oosten (1929) established the following criteria that must be met before checkmarks on scales or bones can be considered annuli: (1) Scales or bones must remain constant in number and identity throughout the life of the fish; (2) growth of the scale or bone must be proportional to the overall growth of the fish; (3) growth checkmarks must be formed at approximately the same time each year; and (4) back-calculated lengths should agree with empirical lengths. The first criterion is fulfilled by using vertebrae as the aging tool.

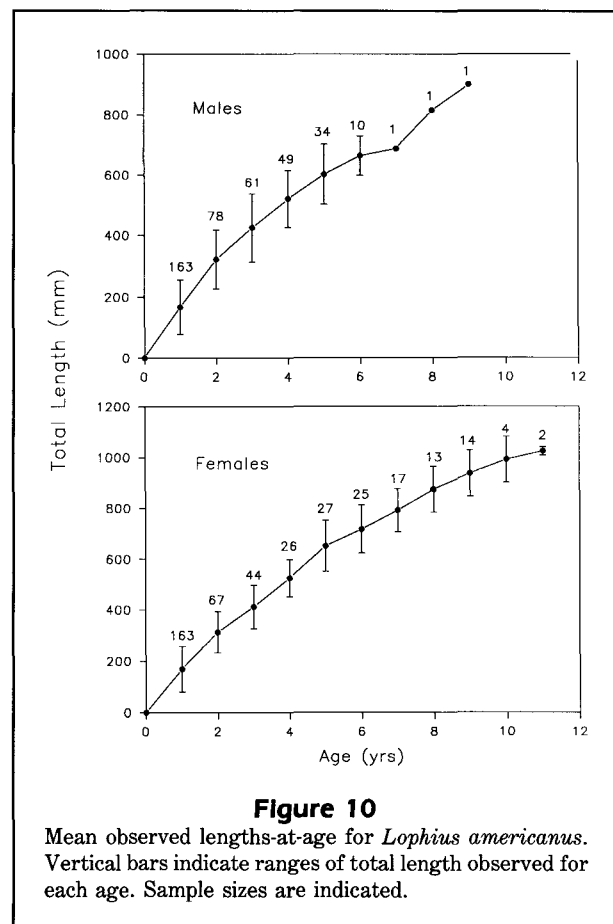
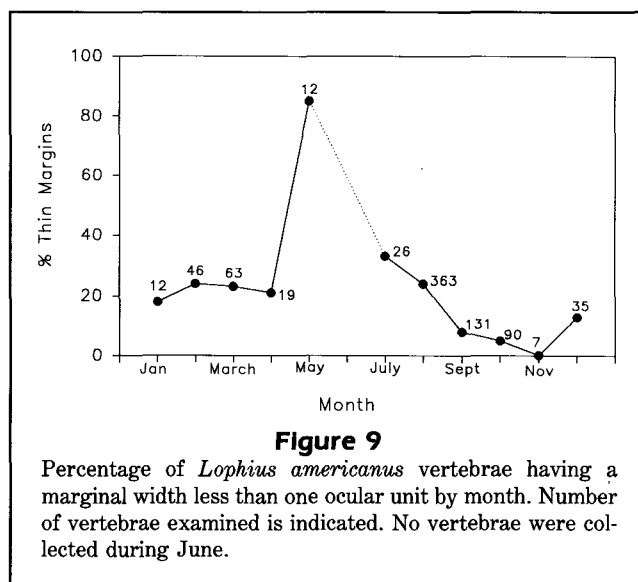


The regression of vertebral radius (VR) on TL revealed a strong linear relationship between the two variables. The regression equation based on 682 vertebrae from both sexes was as follows:

$$TL = 11.077(VR) + 40.018 \quad (r^2 \ 0.97).$$

This indicates that growth of vertebrae is proportional to growth of the fish, thereby satisfying the second criterion.

Monthly mean marginal increments were plotted for all age groups combined (Fig. 8). Sample size was not large enough to plot the age-groups separately. However, inspection of the data indicated that the seasonal progression of marginal increment was similar for all age-groups. Percentage of vertebrae showing a very small marginal increment (less than 1 ocular unit), indicating that little or no growth had occurred since the annulus was deposited, was also plotted (Fig. 9). The annuli were found to be closest to the edge of the vertebrae in May. Marginal increments were highest in December–February, following a period of growth during July–December. The percent of vertebrae with thin margins showed less variation than marginal increments. The percent was highest in May and decreased as the season progressed. These plots indicate that May is the time of annulus formation, and only one checkmark is formed per year. This appears to fulfill the third criterion that states that growth checks must be formed at approximately the same time each year; however, because data were pooled from several years, this cannot be stated with certainty. Although there was a decrease in the marginal increment from February to March, there was no corresponding rise in the percentage of very small margins (i.e., the mean



value of marginal width was not lowered by the presence of marginal widths < 1). Although the relatively small sample sizes preclude making definitive conclusions, these data suggest that some process is causing

Table 3

Observed, von Bertalanffy, and back-calculated lengths-at-age (TL, mm) for male and female *Lophius americanus*, based on counts of vertebral annuli. The number examined for age 1 includes 142 unsexed individuals, which were used in the back-calculations for both sexes.

Age	Number examined	Mean observed length	von Bertalanffy length	Mean back-calculated lengths at successive annuli										
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Males														
1	163	167	133	123										
2	78	322	256	127	267									
3	61	425	367	134	265	374								
4	49	519	469	127	263	377	472							
5	34	602	560	127	269	378	478	568						
6	10	664	644	109	241	352	465	549	634					
7	1	688	719	82	189	284	390	486	592	688				
8	1	815	788	109	255	367	473	602	675	731	793			
9	1	900	850	143	263	396	489	555	621	701	781	860		
			Mean	126	264	374	473	563	633	707	787	860		
		Annual growth increment		126	138	110	100	90	70	74	80	73		
Females														
1	163	169	121	124										
2	67	313	253	126	261									
3	44	412	373	124	257	361								
4	26	526	482	116	248	373	476							
5	27	652	581	130	278	405	507	600						
6	25	718	672	121	250	366	477	580	672					
7	17	792	754	124	265	386	485	573	662	757				
8	13	874	828	110	242	361	468	567	665	745	834			
9	14	937	896	119	250	373	475	567	652	740	821	901		
10	4	991	957	107	244	353	458	574	655	741	815	890	966	
11	2	1024	1014	117	254	380	488	591	677	757	826	894	962	1013
			Mean	123	258	374	483	581	664	748	826	898	965	1013
		Annual growth increment		123	135	116	109	98	83	84	78	72	67	48

the vertebrae to decrease slightly in diameter, possibly the resorption of the outer surfaces due to starvation in late winter.

Mean lengths were back-calculated for 256 males and 260 females. One hundred forty-two individuals, whose sex could not be determined because their gonads were undifferentiated (94–239 mm TL) but who were determined to have one annulus, were included in the back-calculations for each sex, bringing the total number used in the analysis to 398 males and 402 females.

The observed lengths were consistently higher than back-calculated or von Bertalanffy lengths for individual age-groups (Table 3). However, the differences are within the limits of seasonal growth, so the fourth criterion appears to have been fulfilled.

Males and females had very similar lengths-at-age until age 4. Above age 4, the mean lengths for females were slightly greater than males, with the difference becoming more pronounced with increasing age (Fig. 10).

The data suggest a difference in maximum age for the two sexes. The oldest male collected was 9 years

old. Males older than 6 were exceptionally rare. Only one individual from each of the age groups 7, 8, and 9 was captured during the course of this study. The oldest female sampled was 11 years old. Fifty females greater than 6 years old were obtained. It appears that the number of older males is much fewer than females, indicating greater mortality of the males.

Mean back-calculated lengths-at-age were used to develop the vonBertalanffy growth equations. The resulting parameters and equation for females are:

$$\begin{aligned}
 K &= 0.095 \\
 L_{\infty} &= 1576 \text{ mm} \\
 t_0 &= 0.162 \\
 L_t &= 1576.0 (1 - e^{-0.095(t-0.162)}).
 \end{aligned}$$

The growth equation for males was calculated using three slightly different data sets. It was first calculated using all the mean back-calculated lengths available. The equation was then formulated after eliminating the two fish in age-groups 8 and 9 from the data set and finally it was calculated without age-groups 7, 8, or 9.

Because there was only one individual in each of these three oldest age-groups, these were possibly not good estimates of length for these ages. The parameters and equations are as follows.

All males:

$$\begin{aligned} K &= 0.097 \\ L_{\infty} &= 1460.0 \\ t_0 &= 0.015 \\ L_t &= 1460.0 (1 - e^{-0.097(t-0.015)}) \end{aligned}$$

Age-groups 8 and 9 eliminated:

$$\begin{aligned} K &= 0.166 \\ L_{\infty} &= 1018.0 \\ t_0 &= 0.211 \\ L_t &= 1018.0 (1 - e^{-0.166(t-0.211)}) \end{aligned}$$

Age-groups 7, 8, and 9 eliminated:

$$\begin{aligned} K &= 0.157 \\ L_{\infty} &= 1059.0 \\ t_0 &= 0.196 \\ L_t &= 1059.0 (1 - e^{-0.157(t-0.196)}) \end{aligned}$$

The length-weight relationships (Fig. 11) for 305 males and 311 females were:

Males

$$\log_{10} W = 2.833 (\log_{10} TL) - 4.347 \quad (r^2 \ 0.95)$$

Females

$$\log_{10} W = 3.001 (\log_{10} TL) - 4.770 \quad (r^2 \ 0.98)$$

Discussion

Reproduction

All female members of the Lophiiformes are thought to expel nonadhesive, mucoid egg rafts or veils with the possible exception of one species of antenariid angler fish (Pietsch and Grobecker 1980). These veils are buoyant and have a complex structure consisting of individual chambers, which each contain one to three eggs and an opening providing water circulation (Fulton 1898, Gill 1905, Rasquin 1958, Ray 1961). This method of egg production appears to be unique among the fishes.

The goosefishes, *Lophius* spp., have the most spectacular egg veils because of their large size. The egg veil of *L. americanus* can reach 6–12m in length and 0.15–1.5m in width (Martin and Drewry 1978). Several authors have provided detailed description of the egg veils of *L. americanus* (e.g., Agassiz and Whitman 1885, Connolly 1920, Dahlgren 1928) and *L. piscatorius* (Fulton 1898, Bowman 1919).

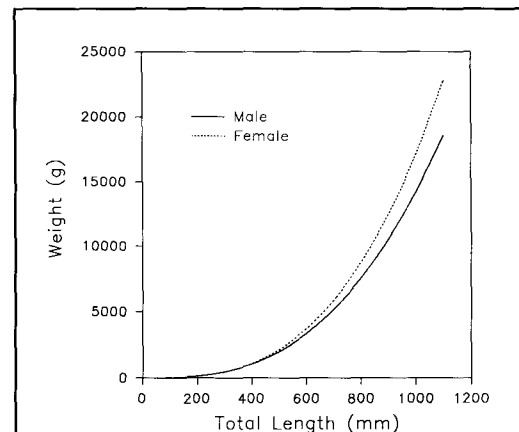


Figure 11

Length-weight relationship for male (n 305) and female (n 311) *Lophius americanus*.

Estimates of fecundity presented by other authors are similar to those obtained in this study. Eaton et al. (1954) estimated 543,000 ova in the ovary of a 660 mm specimen. The regression of fecundity on TL presented here predicts 563,000 ova for a female of this size. Other estimates of fecundity range from 432,000 to 2,670,000 eggs, based on the examination of veils released from females of unknown size (Baird 1871, Nichols and Breder 1927, Berril 1929).

Female goosefish matured at a larger size and at a greater age (487 mm, age 4) than males (369 mm, age 3). This is a common trend among teleosts (Moyle and Cech 1982). In the case of goosefish, the female requires a larger body size to accommodate the large egg veil. Connolly (1920) was unable to determine size-at-maturity because of small sample size, but he stated that a goosefish 18 inches (457 mm) long (unstated sex) was immature, and all individuals over 31 inches (787 mm) were mature. McBride and Brown (1980), in a tabular summary of life-history parameters for several demersal fish species, present the age-at-maturity for *L. americanus* as 4 and 5 years for males and females, respectively. The source of their data is not stated. Martin and Drewry (1978) and several others also suggest that the age of maturity is 4 and 5 years for males and females. They state the source of this information as Connolly (1920). A review of Connolly's paper shows that he was quoting a publication by Fulton (1903), which deals with the growth of *L. piscatorius*, not *L. americanus*. At the time of Connolly's paper, the two species were considered synonymous. *L. piscatorius* is known to reach a larger maximum size and is larger at each age (based on data presented in the following age and growth discussion). The age-at-maturity cannot be considered the same

for the two species; in fact, it would be expected that the age- and length-at-maturity for *L. piscatorius* would probably be greater, as suggested here.

Data on gonad condition and the gonasomatic index indicate that spawning takes place in May–June in the area from Cape Hatteras to Southern New England. Because samples were collected and pooled from throughout this entire region, a seasonal progression of spawning from south to north as suggested in the literature cannot be demonstrated. Testes appear to develop earlier and remain ripe longer than ovaries. Fulton (1898) found the same to be true for *L. piscatorius*. This suggests that males may be multiple spawners. Multiple spawning in males would increase the chances of a ripe female encountering a ripe male, and thereby spawning successfully. It also serves to equalize the energetic investment of the sexes in reproduction. It appears that the investment of females is relatively high. The GSI was as high as 50%. Tsimenidis (1980) found values as high as 37% for the Mediterranean goosfish *L. budegassa*. A large part of the ovarian weight is composed of the mucogelatinous material that forms the veil. The caloric value of this material is unknown, but probably is rather low because of its low density and apparently high water content. However, the large amount of this material, combined with the great number of eggs produced, represents a sizeable energetic contribution by the female to reproduction.

Histological examination of the goosfish testes showed that spermatogenesis and the internal structure are not remarkably different from other teleosts. It also confirmed the validity of macroscopic staging of testes in the field. Examination of ovaries showed that oogenesis is similar to other teleosts but the structure of the ovary is somewhat different. The most significant differences were the presence of stalk-like lamellae containing the developing ova, and epithelium lining the lumen which is responsible for secreting the mucogelatinous matrix. Fulton (1898) was the first to suggest this mechanism of veil formation in the lophiids. His figures and descriptions of the histology of the ovaries of *L. piscatorius* indicate they are identical to those from *L. americanus* seen here. Rasquin (1958) provided detailed descriptions and photographs of the ovaries of two species of antennariid anglers (*Antennarius*, *Histrio*) and one species of ogocephalid angler. These lophiiform species are known to produce egg veils. Although they are all only a fraction of the size of *L. americanus* and *L. piscatorius*, the histology of their ovaries was virtually identical to their larger relatives, including the presence of stalk-like ovigerous lamellae and secretory epithelium. It is reasonable to assume that all members of the order Lophiiformes known to produce egg veils have similar ovaries. This

character may be useful in verifying veil production in some of the deepwater lophiiform families for which veil production has been assumed but not verified.

Pietsch and Grobecker (1980) suggest that the egg veil is an excellent device for broadcasting a large number of eggs over great geographical distances. In addition, the buoyancy of the veil causes the eggs to develop in relatively productive surface waters.

There seem to be additional selective advantages to the egg veil as well. It may function in facilitating fertilization of the eggs. When a veil is first extruded from the female, it absorbs a large quantity of water. As water is absorbed, sperm may be drawn into the egg chambers through the small circulation pores in the veil, thereby insuring fertilization. The veil likely functions by several methods in the protection of the eggs and embryos, since the embryos remain in the egg chamber for 2–3 days after hatching (Dahlgren 1928). Predators such as zooplankton are physically excluded from the egg chambers by the small size of the circulation pore. The veil may reduce or eliminate olfactory cues, thereby eliminating predators locating food items by this method. Wells (1977) suggests that the jelly coat of yellow perch *Perca flavescens* spawn may act in a similar manner. Finally, the mucogelatinous material of goosfish egg veils may be toxic or repugnant to potential predators. Newsome and Tompkins (1985) found that the egg mass of yellow perch contain some compound(s) that are not toxic but seem to deter predators. While such a protective device is rare among teleosts (Fuhrman et al. 1969, Orians and Janzen 1974), the presence of toxic or unpalatable compounds within the jelly coat of amphibian egg masses is well known (Licht 1969, Ward and Sexton 1981).

Age and growth

Females and males have about the same weight-at-length before maturity. After maturity the females are slightly heavier than males because of their large ovaries. As the ovaries ripen, weight differences between males and females become greater. The regression slopes for males and females approximate 3, implying isometric growth in the length-weight relationship. Tsimenidis and Ondrias (1980) calculated very similar length-weight regressions for *L. piscatorius* in the Mediterranean Sea.

Vertebrae appear to be valid aging tools for *L. americanus*. They satisfy all of Van Oosten's (1929) criteria. Vertebrae can readily be located and removed from goosfish and are relatively easy to prepare and read. The annuli are readily discernible since only 3% of the vertebrae were considered unreliable, and an inexperienced, independent reader agreed with the counts in 80% of the readings he performed.

These data indicate that the annuli become discernible in May. Because these rings are present on juveniles as well as adults, they appear to be related to seasonal patterns of growth rather than reproduction. The annuli are difficult to see when they are at the very edge of the vertebral centra. For this reason, they are probably not detected until some additional growth has occurred after they are laid down. Yasuda (1940) has shown that on vertebrae of *Scombrops* sp. annuli were formed 1.5 months later than on the otoliths. So it is likely that the annuli (composed of a step and a translucent band) found on goosfish vertebrae represent the end of fast growth (the step) in late-fall and a period of slow winter growth (the translucent band).

While several authors have studied growth in *L. piscatorius* and *L. budegassa* (Fulton 1903, Guillou and Njock 1978, Tsimenidis and Ondrias 1980), only Connolly (1920) has looked at growth in *L. americanus*. He based his growth estimates on vertebral annuli counts, but his sample size was only six individuals. His results were as follows: age 1, 114mm; age 4, 457mm; age 8, 737mm; age 9, 787mm; age 10, 940mm; age 12, 1016mm. These estimates are slightly lower than found in this study, but a slower growth rate would be expected in the colder Canadian waters in which Connolly conducted his study.

The growth rate of *L. americanus* is intermediate to *L. piscatorius* and *L. budegassa*. Figure 12 compares the mean back-calculated lengths for the two European species (from Tsimenidis and Ondrias 1980) with data presented here for *L. americanus*.

The differences in observed and back-calculated mean lengths between males and females past age 4 are small, but appear to be real. This is the most common form of sexual dimorphism among fishes (Moyle and Cech 1982). Tsimenidis and Ondrias (1980) found similar small differences between the sexes for *L. budegassa* and *L. piscatorius*.

More significant is the difference in mortality between the sexes implied by the data. The heavier mortality of males may be caused by increased predation due to their smaller size, but this does not seem likely. Perhaps the males exhibit behavioral or distributional differences which make them more susceptible to predation or fishing effort. A final possibility is that they simply reach senescence before females.

The von Bertalanffy growth equations fit the back-calculated lengths extremely well. The values for L_{∞} for both sexes seem somewhat inflated. The maximum reported size for *L. americanus* is approximately 1220mm (Bigelow and Schroeder 1953). The largest female collected in this study was 1115mm and the calculated L_{∞} was 1576mm. The largest male collected was 900mm compared with a calculated L of 1018–1460mm. The inflation of L_{∞} is caused by a lack of

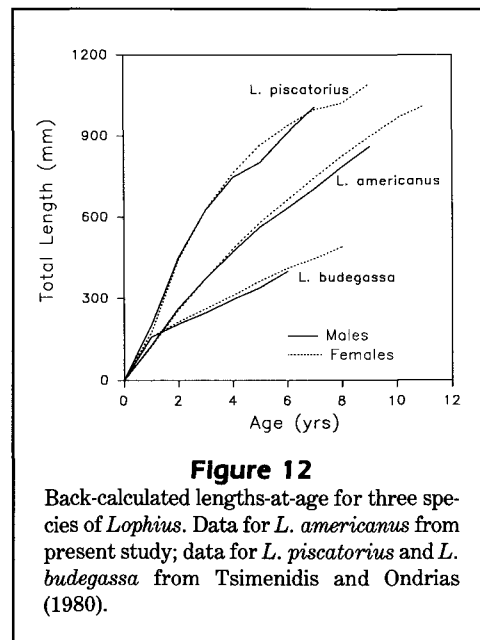


Figure 12

Back-calculated lengths-at-age for three species of *Lophius*. Data for *L. americanus* from present study; data for *L. piscatorius* and *L. budegassa* from Tsimenidis and Ondrias (1980).

representatives from the older age-classes. This is a common problem in age and growth studies. The asymptotic length is therefore not well defined for either sex in this study. The sampling effort was believed to be intense enough to sample these larger individuals if they were present in the population. It is concluded that these individuals are simply not present. This may be the result of commercial fishing pressure (groundfishing and scalloping), which tends to be selective towards larger individuals.

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Citations

- Agassiz, A., and C.O. Whitman**
 1885 Studies from the Newport Marine Laboratory, XVI. The development of the osseous fishes. Part I. The pelagic stages of young fishes. Mem. Mus. Comp. Zool. 14(1):1-56.
- Baird, S.F.**
 1871 Spawning of the goosefish *L. americanus*. Am. Nat. 5:785-786.
- Berril, N.J.**
 1929 The validity of *L. americanus* as a species distinct from *L. piscatorius* with notes on rate of development. Contrib. Can. Biol. Fish. 4(12):143-155.
- Bigelow, H.B., and W.C. Schroeder**
 1953 Fishes of the Gulf of Maine. U.S. Fish. Wildl. Serv. Fish. Bull. 53(74), 577 p.
- Bowman, A.**
 1919 The eggs and larvae of the angler (*Lophius piscatorius*) in Scottish waters. Rep. Fish. Board Scotl. Sci. Invest. for 1919, No. 1. 42 p.
- Caruso, J.H.**
 1975 Sexual dimorphism of the olfactory organs of lophiids. Copeia 1975:380-381.
 1977 The systematics of the fish family Lophiidae. Ph.D. diss., Tulane Univ., New Orleans, 220 p.
 1983 The systematics and distribution of the lophiid angler fishes: II. Revision of the genera *Lophiomus* and *Lophius*. Copeia 1983:11-30.
- Connolly, C.J.**
 1920 History of the new food fishes. III. The angler. Bull. Biol. Board Can. 3:1-17.
- Cuvier, G., and A. Valenciennes**
 1837 Historie naturelle des poissons, vol. 12. F.G. Levrault, Paris, 507 p.
- Dahlgren, U.**
 1928 The habits and life history of *Lophius*, the angler fish. Nat. Hist. 28(1):18-32.
- Eaton, T.H. Jr., C.A. Edwards, M.A. McIntosh, and J.P. Rowland**
 1954 The structure and relationships of the anglerfish, *Lophius americanus*. J. Elisha Mitchell Sci. Soc. 70(2):205-218.
- Edwards, R.L.**
 1965 Relation of temperature to fish abundance and distribution in the southern New England area. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6:95-110.
- Fuhrman, F.A., G.J. Fuhrman, D.L. Dull, and H.S. Moser**
 1969 Toxins from eggs of fishes and amphibia. J. Agric. Food Chem. 17:417-424.
- Fulton, T.W.**
 1898 The ovaries and ovarian eggs of the angler or frog fish (*Lophius piscatorius*) and of the John Dory (*Zeus faber*). Sixteenth Annu. Rep. Fish. Board Scotl. 3:125-137.
 1903 The distribution, growth, and food of the angler. Twenty-first Annu. Rep. Fish. Board Scotl. 3:186-199.
- Gill, T.**
 1905 The life history of the angler. Smithson. Misc. Collect. 47(4):500-516.
- Grosslein, M.D., and T.R. Azarovitz**
 1982 Goosefish, *Lophius americanus*. In Fish distribution. MESA N.Y. Bight Atlas Monogr. 15, New York Sea Grant Inst., Stony Brook.
- Guillou, A., and J.C. Njock**
 1978 Analyse des structures de la peche dans les parts de la cote atlantique francaise de 1961 a 1975 et des incidences du chalutage sur les stocks des principales especes concernees par cette activite dans les mers adjacentes. Revue Trav. Inst. Peches Marit. 42(1, 2):120-128 [in French].
- Hildebrand, S.F., and W.C. Schroeder**
 1928 Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, pt. 1, 388 p.
- Hyder, M.**
 1969 Histological studies on the testes of *Tilapia leucesticta* and other species of the genus *Tilapia* (Pisces:Teleostei). Trans. Am. Microsc. Soc. 88(2):211-231.
- Jean, Y.**
 1965 Seasonal distribution of monkfish along the Canadian Atlantic mainland. J. Fish. Res. Board Can. 22(2):621-624.
- Lagler, K.F.**
 1956 Freshwater fishery biology, 2d ed. W.C. Brown, Dubuque, 248 p.
- Lawler, E.F. Jr.**
 1976 The biology of the sandbar shark, *Carcharinus plumbeus*, in the lower Chesapeake Bay and adjacent waters. M.A. thesis, College of William and Mary, Williamsburg, 48 p.
- Lewis, W.M.**
 1949 The use of vertebrae as indicators of the age of the northern black bullhead, *Ameriurus m. melas*. Iowa State Coll. J. Sci. 22(2):209-218.
- Licht, L.E.**
 1969 Palatability of *Rana* and *Hyla* eggs. Am. Midl. Nat. 82:296-298.
- Lyczkowski, J.M.**
 1971 Age and growth of the northern puffer, *Sphoeroides maculatus*. M.A. thesis, College of William and Mary, Williamsburg, 26 p.
- Markle, D.F., and J.A. Musick**
 1974 Benthic-slope fishes found at 900 m depth along a transect in the western North Atlantic Ocean. Mar. Biol. (Berl.) 26: 225-233.
- Martin, F.D., and G.E. Drewry**
 1978 Lophiidae. In Development of fishes of the mid-Atlantic Bight—An atlas of egg, larval and juvenile stages, vol. 6, Stromateidae through Ogocephalidae, p. 357-366. U.S. Fish Wildl. Serv. OBS 78/12, 416 p.
- McBride, M.M., and B.E. Brown**
 1980 The status of the marine fishery resources of the northeastern United States. NOAA Tech. Memo. NMFS-F/NEC-5, Northeast Fish. Sci. Cent., Woods Hole, 13 p.
- McKenzie, R.A.**
 1936 Some notes on the monkfish or angler (*Lophius piscatorius*). Can. Field Nat. 50:55-56.
- Mercer, L.P.**
 1978 The reproductive biology and population dynamics of black sea bass, *Centropristis striata*. Ph.D. diss., College of William and Mary, Williamsburg, 196 p.
- Moyle, P.B., and J.J. Cech Jr.**
 1982 Fishes, an introduction to ichthyology. Prentice-Hall, Englewood Cliffs, 593 p.
- Newsome, G.E., and J. Tompkins**
 1985 Yellow perch egg masses deter predators. Can. J. Zool. 63:2882-2884.
- Nichols, J.T., and C.M. Breder**
 1927 The marine fishes of New York and southern New England. Zoologica (NY) 9(1):1-192.

Northeast Fisheries Science Center

- 1991 Status of the fishery resources off the northeastern United States. NOAA Tech. Memo. NMFS-F/NEC-86, Northeast Fish. Sci. Cent., Woods Hole, 132 p.
- Orians, G.H., and D.H. Janzen**
1974 Why are embryos so tasty? *Am. Nat.* 108:581-592.
- Pietsch, T.W., and D.B. Grobecker**
1980 Parental care as an alternative reproductive mode in an antennariid angler fish. *Copeia* 1980:551-553.
- Proctor, W., H.C. Tracy, E. Helwig, C.H. Blake, J.E. Morrison, and S. Cohen**
1928 Fishes—A contribution to the life history of the angler (*Lophius piscatorius*). In *Biological survey of the Mount Desert Region, Part 2*, p. 1-29, Philadelphia.
- Rasquin, P.**
1958 Ovarian morphology and early embryology of the pediculate fishes *Antennarius* and *Histrio*. *Bull. Am. Mus. Nat. Hist.* 114(4):331-371.
- Ray, C.**
1961 Spawning behavior and egg raft morphology of the ocellated fringed frogfish, *Antennarius numifer* (Cuvier). *Copeia* 1961:230-231.
- Ricker, W.E.**
1975 Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 p.
- Ross, J.L.**
1978 Life history aspects of the gray tilefish, *Caulolatilus microps* (Goode and Bean, 1878). M.A. thesis, College of William and Mary, Williamsburg, 120 p.
- Scott, W.B., and M.G. Scott**
1988 Atlantic fishes of Canada. *Can. Bull. Fish. Aquat. Sci.* 219, 731 p.
- Simpson, A.C.**
1951 The fecundity of the plaice. *Fish. Invest. Ser. 2, Mar. Fish. G.B. Minist. Agric. Fish. Food* 17(5), 27 p.
- Tsimenidis, N.Ch.**
1980 Contribution to the study of the angler-fishes *Lophius budegassa* Spinola, 1807 and *L. piscatorius* L., 1758 in Greek seas. *Inst. Oceanogr. Fish. Res. (Athens) Spec. Publ.* 4: 180-190.
- Tsimenidis, N.Ch., and J.Ch. Ondrias**
1980 Growth studies on the angler-fishes *L. piscatorius* and *L. budegassa* in Greek waters. *Thalasographica* 2(3):63-94.
- Van Oosten, J.**
1929 Life history of the lake herring (*Leucichthys artedi*, LeSeur) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bull. U.S. Bur. Fish.* 44:265-428.
- Ward, D., and O.J. Sexton**
1981 Anti-predator role of salamander egg membranes. *Copeia* 1981:724-726.
- Wells, L.**
1977 Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954-75. *J. Fish. Res. Board Can.* 34: 1821-1829.
- Wenner, C.A.**
1978 *Lophius americanus*. In *Making a living on the continental slope and in the deep sea: Life history of some dominant fishes of the Norfolk Canyon area*, p. 253-263, 267-268. Ph.D. diss., College of William and Mary, Williamsburg.
- Yasuda, H.**
1940 On the rings formed on scale, vertebral centrum, and otolith of the same individual fish. *Jpn. Soc. Sci. Fish. Bull.* 8:290-300.